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**DINOFLAGELLATE ASSOCIATIONS IN A CORAL REEF-MANGROVE
ECOSYSTEM: PELICAN AND ASSOCIATED CAYS, BELIZE**

BY

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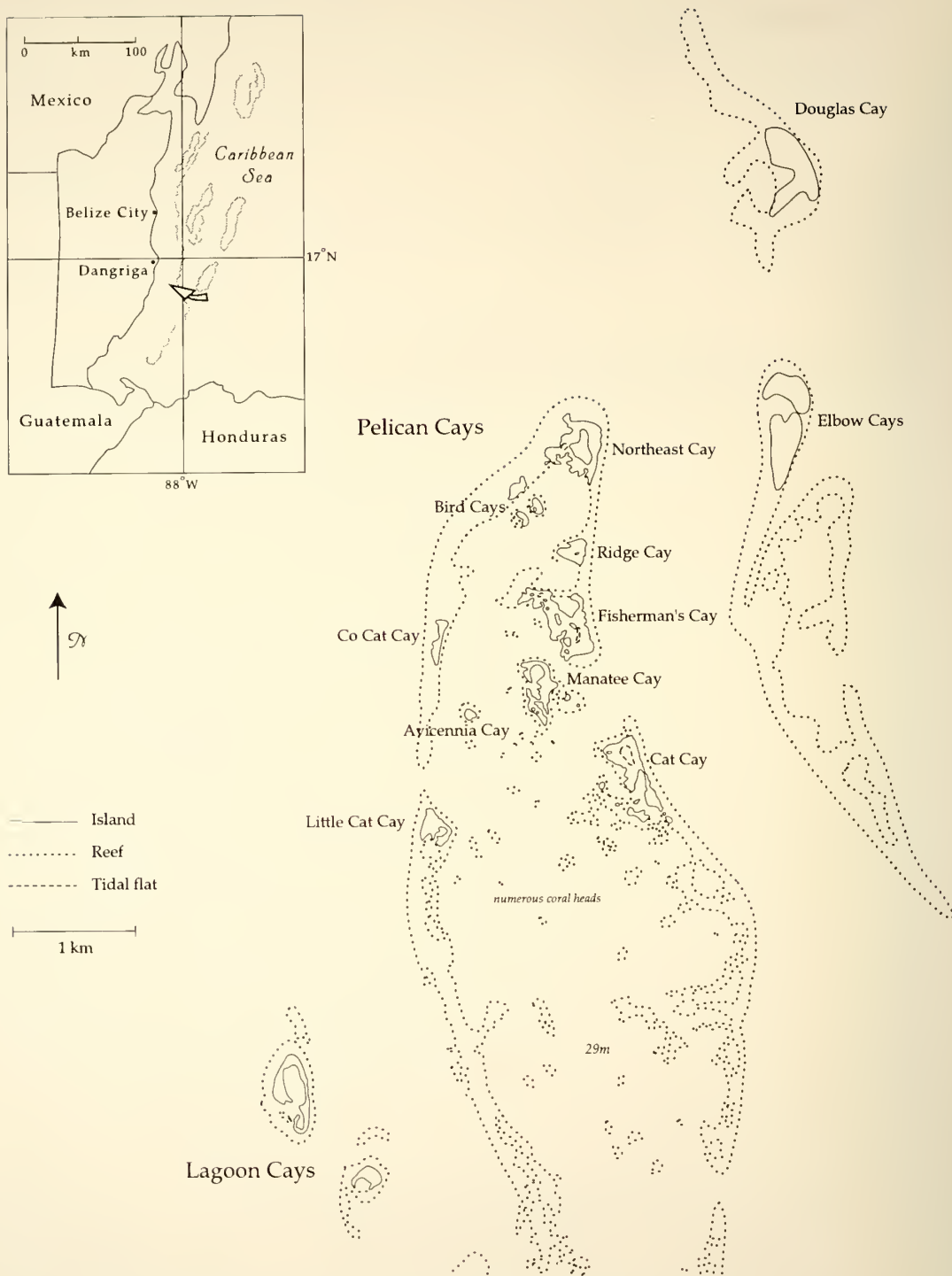


Figure 1. Index map showing the location of the Pelican and associated cays

DINOFLAGELLATE ASSOCIATIONS IN A CORAL REEF-MANGROVE ECOSYSTEM: PELICAN AND ASSOCIATED CAYS, BELIZE

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ABSTRACT

Information on the population structure of dinoflagellate taxa has been obtained from a 1994-96 study of planktonic, benthic, and oceanic dinoflagellates in the coral reef-mangrove ecosystem at Pelican Cays, Belize, and at nearby cays. Seventy-two samples were collected at six sites: Cat Cay, Douglas Cay, Elbow Cay, Fisherman's Cay, Lagoon Cay and Manatee Cay. Up to 95% of the organisms in the >20- μ m microplankton samples consisted of armored dinoflagellates from 110 species in 33 genera. Of these species, 80 were photosynthetic, 30 heterotrophic, and 12 mixotrophic. Maximum cell concentrations were observed for *Dinophysis caudata*, *Gymnodinium sanguineum*, and *Protoperidinium divergens*. Dominant taxa included 16 *Protoperidinium* species, 11 *Gonyaulax* species, and 10 *Ceratium* species. Only 6 planktonic and 16 benthic species were harmful, toxin-producing dinoflagellates. Bloom-forming taxa included *Ceratium furca* and *Gonyaulax polygramma*. The findings illustrate the richness and biodiversity of dinoflagellate assemblages within the study area, as well as the importance of dinoflagellates in the microscopic food web.

INTRODUCTION

Dinoflagellates in coral reef-mangrove ecosystems dwell in plankton, patch reefs, seagrass beds, and sand and on the surface of macroalgae. Hence they have a complex ecology. The south central lagoon of the Belizean Barrier Reef is an oceanic coral reef-mangrove boundary environment containing a network of coral ridges and semi-enclosed or enclosed ponds, some with mangrove covers (Macintyre et al., this volume). This ecosystem, though small in geographic scale, is characterized by great typological diversity. Biological communities within this system vary markedly from one pond to another. Because of this complexity and the lack of detailed observations, few generalizations have been made about dinoflagellate distribution in Belizean coral reef-mangroves. Some important details about the associations of species in ecologically diverse environments have come to light as a result of two-week surveys of dinoflagellate species composition and abundance conducted annually from 1994 to 1996 in Pelican and nearby cays. Earlier studies have provided only limited insight into planktonic dinoflagellate associations from the southeast Caribbean Sea (Halim, 1967; Hulburt, 1968; Marshall, 1973). This discussion presents comparative information on the distribution of

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dinoflagellates at six sites in the oceanic environment of Pelican Cays (Cat Cay, Fisherman's Cay, Lagoon Cay, and Manatee Cay), at nearby Douglas and Elbow Cays, and at detritus-driven Twin Cays, north of Pelican Cays.

METHODS

The Pelican Cays, Belize, are composed of Holocene lagoon reefs (Purdy, 1994) colonized by red mangroves, *Rhizophora mangle*. Cut by deep channels, these reefs form a number of shelf atolls (James and Ginsburg, 1979) and an unusual network of reef ridges, both submerged and exposed (Macintyre et al., this volume). The ponds are deep in the center, have eroded peat banks round the margin, and are separated by coral ridges. Crystal clear water allows corals to proliferate adjacent to mangrove prop roots. With little water exchange from the ocean side, the ponds are warmer and more saline than usual, and could be considered separate water masses (Villareal et al., this volume).

Cells were collected from six sites at the Pelican Cays and nearby: Cat Cay, Douglas Cay, Elbow Cay, Fisherman's Cay, Lagoon Cay, and Manatee Cay (Fig.1). Study sites were selected for their varied phytoplankton associations. Seventy-two samples were gathered during yearly field trips in May between 1994 and 1996: 42 from Manatee Cay, 6 from Cat Cay, 8 from Douglas Cay, 6 from Elbow Cay, 7 from Fisherman's Cay, and 3 from Lagoon Cay. The water temperature ranged from 26.5 to 30.6°C. Salinity levels ranged from 32 to 35.7 ‰.

Samples were collected just below the water surface using a 20-µm pore size plankton net towed by a small boat at the lowest speed for 5 min. The net was fitted with a calibrated flow meter to estimate the volume of water entering the net. Samples were concentrated to 100-ml volume and fixed with 1% glutaraldehyde final concentration (Faust, 1990). Dinoflagellates were enumerated in a 1-ml Sedwick-Rafter counting chamber using three replicates for each sample (Guillard, 1973). Cells were identified and measured (at least 20 cells) at 630x magnification with a Carl Zeiss Axiophot light microscope. The dinoflagellate specimens generated by this study are deposited in the Dinoflagellate Collection of the U.S. National Herbarium, Smithsonian Institution, Washington, D.C.

RESULTS

Dinoflagellate assemblages at and near Pelican Cays included coastal benthic and oceanic species, whereas the majority of those at Twin Cays were benthic. The majority at Pelican Cays were autotrophic and oceanic, with some neritic in origin (Table 1). Eighty species were planktonic and 30 species were benthic; both toxic and nontoxic species were present. Of the 110 dinoflagellates, 11 species are most likely new and have yet to be described. I identified 51 species from Manatee Cay, 39 from Douglas Cay, 19 from Cat Cay, 15 from Elbow Cay, 13 from Lagoon Cay, and 11 from Fisherman's Cay. The highest numbers of species were found in samples collected from Manatee and Douglas Cays, while the lowest numbers were found in Lagoon and Fisherman's Cays (Appendix).

Table 1. Distribution of dinoflagellate species in the Pelican and associated Cays.

Taxa	Planktonic		Benthic		Auto-trophs	Hetero-trophs
	Total	Toxic	Total	Toxic		
<i>Amphidinium</i>	1		1	1	1	
<i>Blepharocysta</i>	1					1
<i>Bysmatrum</i>			2		2	
<i>Ceratium</i>	10				10	
<i>Cochlodinium</i>	1	1			1	
<i>Coolia</i>			1	1	1	
<i>Corythodinium</i>	1					1
<i>Dinophysis</i>	6	3			3	3
<i>Diplopetta</i>	2					2
<i>Diplosalis</i>	3					3
<i>Diplosalopsis</i>	1					1
<i>Gambierdiscus</i>			4	4	4	
<i>Goniodoma</i>	1				1	
<i>Gotoius</i>	1					1
<i>Gonyaulax</i>	11	1			11	
<i>Gymnodinium</i>	4				4	
<i>Heteraulacus</i>	1				1	
<i>Lingolidinium</i>	1				1	
<i>Ostreopsis</i>			5	3	5	
<i>Noctiluca</i>	1				1	
<i>Peridinium</i>	3				3	
<i>Peridiniella</i>	1				1	
<i>Phaeopolykrik</i>	1				1	
<i>Plagodinium</i>	1				1	
<i>Prorocentrum</i>	3		14	7	17	
<i>Podolampas</i>	2					2
<i>Protoceratium</i>	2				2	
<i>Protoperidinium</i>	16				1	15
<i>Pyrodinium</i>	2	1			2	
<i>Pyrophacus</i>	3				3	
<i>Scrippsiella</i>			2		2	
<i>Sinophysis</i>			1			1
<i>Zygabikonidi</i>	1					1

Dinoflagellate assemblages in the Pelican Cays were diverse. They included coastal planktonic and benthic species and oceanic offshore species (Fig. 2). Cosmopolitan species were *Ceratium furca* and *C. tripos*, *Dinophysis caudata*, *Gonyaulax spinifera*, *Prorocentrum micans*, and *Protoperidinium depressum*. Common species were *Gonyaulax spinifera* and *Protoperidinium* sp. cf. *steinni*. Tropical offshore forms included *Pyrodinium bahamense* var.

bahamense and *P. bahamense* var. *compressum*; an upwelling indicator species, *Ceratium symmetricum*; and two rare species, *Gonyaulax scrippsiae* and *Protoperidinium steinii* (Appendix).



Figure 2. Number of species in the dinoflagellate genera recorded in Pelican Cays and Twin Cays.

Dinoflagellate assemblages from 33 genera were identified in the Pelican Cays ecosystem (Table 1). Dinoflagellate species are listed in the Appendix. Seventy-nine autotrophic species were from the following genera: *Amphidinium*, *Bysmatrum*, *Ceratium*, *Cochlodinium*, *Coolia*, *Dinophysis*, *Goniodoma*, *Gambierdiscus*, *Gonyaulax*, *Noctiluca*, *Gymnodinium*, *Heteracaulus*, *Lingolodinium*, *Ostreopsis*, *Peridinium*, *Peridiniella*, *Phaeopolykrikos*, *Plagodinium*, *Prorocentrum*, *Protoceratium*, *Pyrodinium*, *Pyrophacus*, and *Scrippsiella*. Thirty-one heterotrophic species were from the following genera: *Blepharocystis*, *Corythodinium*, *Ceratium*, *Dinophysis*, *Diplosalis*, *Diplopelta*, *Diplopsalopsis*, *Protoperidinium*, *Podolampas*, and *Zygabiokonidium*. Thirty benthic species were from the following genera: *Amphidinium*, *Coolia*, *Bysmatrum*, *Gambierdiscus*, *Ostreopsis*, *Prorocentrum*, *Scrippsiella*, and *Sinophysis*. Twelve mixotrophic species were from the following genera: *Ostreopsis*, *Gambierdiscus*, *Prorocentrum*, and *Pyrophacus* (Faust, 1998). Of the 12 mixotrophic species, 11 are known to be toxic: *Ostreopsis* (Norris et al., 1985), *Gambierdiscus* (Durant-Clement, 1987), and *Prorocentrum* (Murakami et al., 1982).

In contrast, a total of 30 species and 14 genera were identified at Twin Cays. These included 27 autotrophic species. Twelve species were in the genus *Prorocentrum* and others in the following genera: *Amphidinium*, *Bysmatrum*, *Ceratium*, *Cochlodinium*, *Gambierdiscus*, *Coolia*, *Dinophysis*, *Gonyaulax*, *Gymnodinium*, *Lingolodinium*, *Plagiodinium*, *Protoperidinium*, and *Scrippsiella*. Two species were heterotrophic: *Dinophysis rotundata* and *Sinophysis microcephalus* (Table 1; Appendix; Faust, 1996).

Few toxic species were found at Pelican Cays (Fig. 3). Of the 110 species identified, 22 are known toxin-producers: 6 of these are planktonic species and 16 are benthic species (Table 1). The number of toxic species varied in each cay. The number was higher in nutrient-enriched environments: 14 species in Manatee Cay, 12 in Douglas Cay, and 11 in Elbow Cay. Numbers were lower in oligotrophic waters: 5 species in Cat Cay, 4 in Fisherman's Cay, and 3 in Lagoon Cay. In contrast, of the 30 species at Twin Cays, 12 were toxic (Fig. 3). Although toxic species were low at both Pelican Cays and Twin Cays, toxic populations of dinoflagellates appear to be an endemic part of Belizean mangrove ponds. The low level of toxic populations in the Southern Belizean Barrier Reef ecosystem probably prevents toxic outbreaks of ciguatera (Yasumoto et al., 1987). The most abundant dinoflagellates were cosmopolitan species (Fig. 4). Cell numbers were an order of magnitude lower at Pelican Cays than at Twin Cays. At Manatee Cay, three autotrophic species exhibited maximum cell numbers: *Ceratium furca* (10,700 cells/L), *Gymnodinium sanguineum* (2,000 cells/L), and *Dinophysis caudata* (3,200 cells/L). One oceanic heterotrophic species also had elevated cell numbers: *Protoperidinium divergens* (1,050 cells/L). At Twin Cays, benthic autotrophic species were most abundant: *Bysmatrum subsalsum* (syn.=*Scrippsiella subsalsum*) (18,500 cells/L), *Prorocentrum belizeanum* (17,800 cells/L), *Prorocentrum elegans* (14,500 cells/L), and *Prorocentrum mexicanum* (10,500 cells/L). These cell populations were attached to floating detritus in protected embayments in the early afternoon on sunny and windless days. Two species, *P. belizeanum* (Morton et al., 1998) and *P. mexicanum* (Nakajima et al., 1981) have been shown to produce the toxin okadaic acid. At Pelican Cays, two autotrophic species developed "red tide" levels on three occasions, causing discoloration of the waters: at Manatee Cay, in Lagoon B, *Ceratium furca* reached a cell density >100,000 cells/L during May 1996 (Morton, in press); and at Douglas Cay, *Gonyaulax polygramma* reached concentrations of 3.5 million cells/L in May 1995, and 1.8 million cells/L in May 1996 (Morton and Villareal, in press). Both cays are nutrient enriched owing to resident pelican colonies.

Pelican droppings most likely create the elevated levels of organic nutrients needed to support the development of such high cell concentrations.

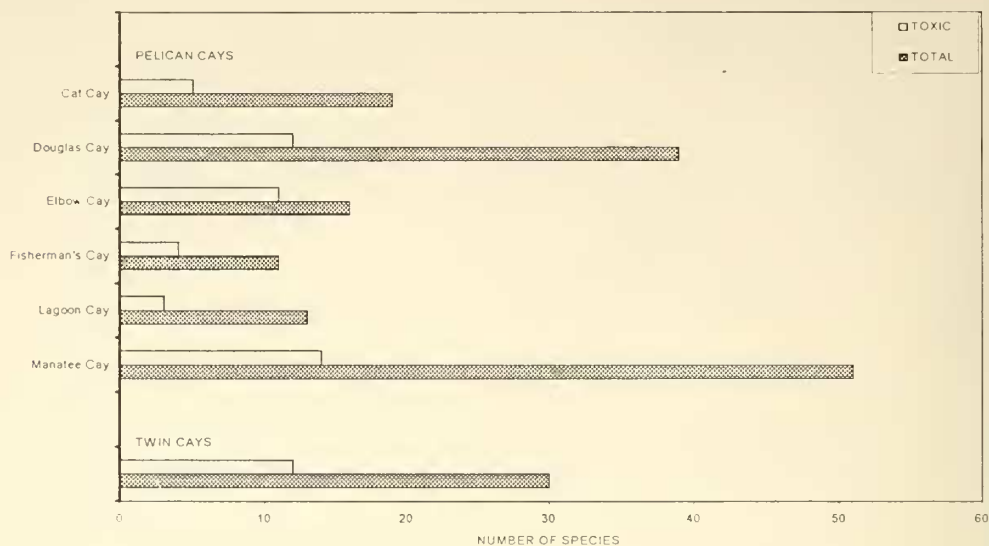


Figure 3 The total number of toxic and non-toxic dinoflagellate species at Pelican Cays and Twin Cays

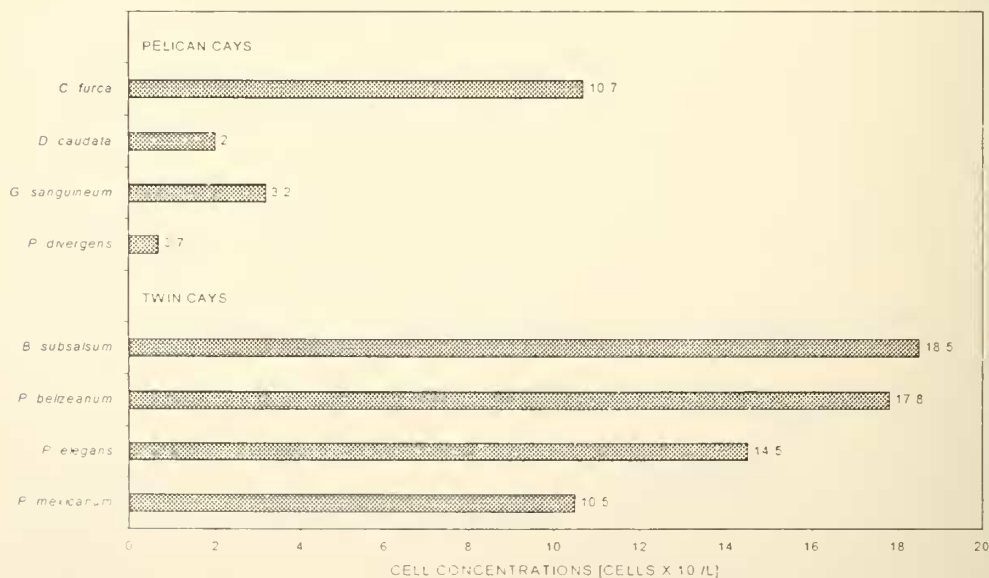


Figure 4 Cell concentrations of most abundant dinoflagellate species at Pelican Cays and Twin Cays

DISCUSSION

Dinoflagellate assemblages in warm coastal waters are planktonic oceanic species (Steidinger and Williams, 1970). However, the Pelican Cays mangrove ecosystem possesses diverse assemblages that include coastal planktonic, benthic, and oceanic offshore species. Armored dinoflagellates account for 95% of these populations. Unarmored forms include only six species in three genera: *Cochlodinium*, *Gymnodinium*, and *Phaeopolykrikos* (Appendix; Steidinger and Williams, 1970). The presence of oceanic species in the studied cays is an unexpected finding. Assemblages in the area inhabit ponds, which are virtually closed by coral ridges (Macintyre et al., this volume) that limit water exchange with the open ocean except during storms or extreme high tides (Villareal et al., this volume). It is difficult to ascertain whether the oceanic forms are indigenous to the Pelican Cays ecosystem or were introduced from fore-reef waters via surface currents or other means. At Twin Cays, benthic dinoflagellates are a dominant component of the dinoflagellate assemblage (Faust, 1996). They are associated with detritus (Faust and Gullede, 1996) attached to macroalgal surfaces (Morton and Faust, 1997) and form a mucilaginous matrix (Faust, 1996).

Oligotrophic waters at Pelican Cays maintain a remarkably abundant and diverse population of dinoflagellates belonging to at least 110 species. About 50% of the total species identified in this study appear to be new reports in the Belizean Barrier Reef ecosystem. However, diversity varied among the six collection sites (Table 1, Appendix, Figures 5, 6). At Elbow Cay, for example, the majority of species were autotrophic benthic, whereas at Cat Cay they were autotrophic planktonic. The highest number of species was found at Manatee Cay, which included autotrophic planktonic and benthic species, along with heterotrophic planktonic species (Table 1).

Dinoflagellate diversity in Pelican Cays differs greatly from that reported in deep offshore neritic waters of the eastern Caribbean Sea (Halim, 1967; Hulburt, 1968; Marshall, 1973). The results of this study suggest that dinoflagellate abundance may be related to nutrient enrichment, as affected by the topography of each lagoon (Macintyre et al., this volume), and to the presence of an abundant *in situ* attached biotic component (Rützler and Feller, 1996). The significant differences in the dinoflagellate associations at Pelican Cays and at Twin Cays (Faust, 1996) illustrate the complex ecology, species richness, biodiversity, and varied taxonomy of dinoflagellates in the coral reef-mangrove ecosystem at Belize.

Oligotrophic waters at Manatee Cay exhibited three levels of dinoflagellate cell concentrations and nutrient enrichment. In the first instance, cell levels were $>1,000$ cells/L, a moderately enriched condition; the autotrophic species *Ceratium furca*, *Dinophysis caudata*, and *Gymnodinium sanguineum*, and the heterotrophic species *Proroperidinium divergens* were often present. In the second instance, cell levels were $>100,000$ cells/L, a highly enriched situation; *C. furca* was a bloom former (Morton, this volume). In the third instance, cell levels of many species were $<1,000$ cells/L, the most common situation. The high cell densities of *C. furca* were unusual. However, macroalgae, phytoplankton, invertebrates, and filter feeders were all abundant, and a constant source of dissolved nutrients (Smayda, 1991). At Twin Cays the available dissolved nutrients, originating from the decomposition of detritus, cause nutrient-enriched waters and the development of blooms (Faust, 1996).

Smayda (1991) suggests that algal blooms are natural events and that elevated cell concentrations relate to local anthropogenic nutrient enrichment. In the Pelican Cay ecosystem,

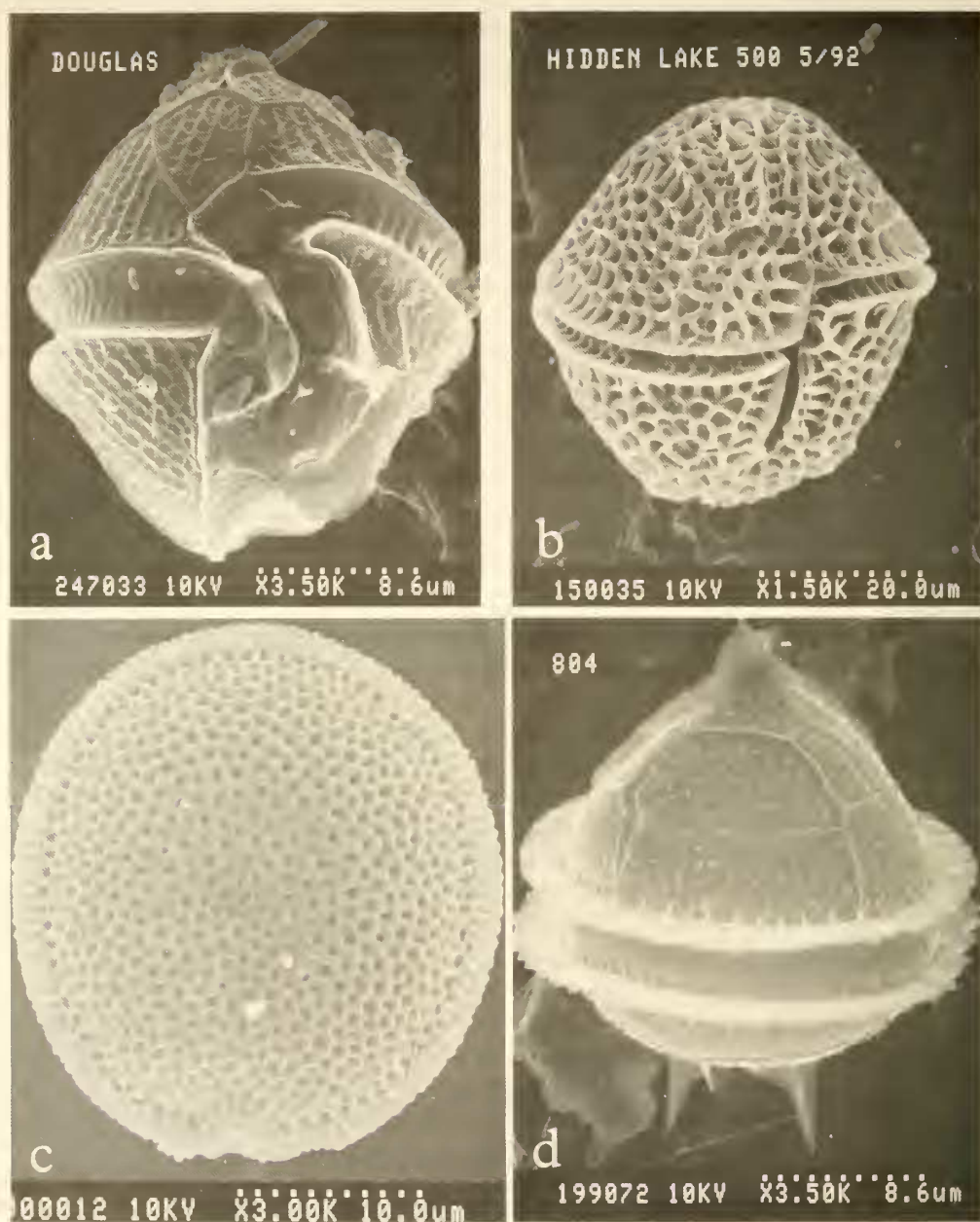


Figure 5. Dinoflagellate species identified from the Pelican Cays sampling area (scanning electron micrographs; refer to the Appendix): a, *Bysmatrum caponii*; b, *Gonyaulax grindleyi*; c, *Prorocentrum ruetzlerianum*; d, *Protoperidinium pyrum*.

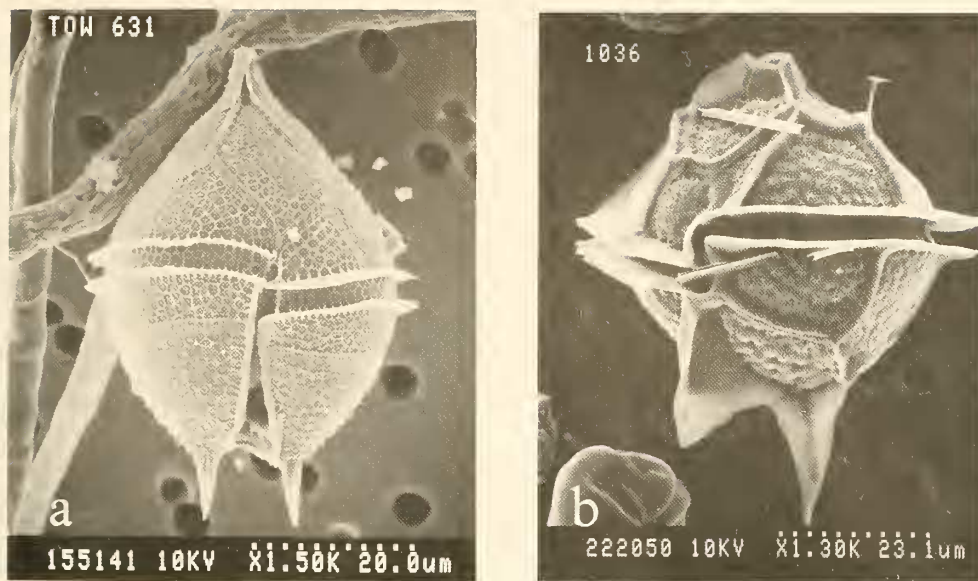


Figure 6. Dinoflagellate species identified from the Pelican Cays sampling area (scanning electron micrographs; refer to the Appendix): a, *Protoperidinium* sp. cf. *steinii*; b, *Pyrodinium bahamense* var. *bahamense*.

dissolved organic nutrient enrichments could originate from numerous sources in addition to microalgal assemblages: the mangrove forest, corals, seagrass beds, macroalgal meadows, and peat walls dominated by filter-feeding invertebrates and macroalgae (Rützler and Feller, 1996). In selected enclosed lagoons such as Manatee Cay, dissolved nutrients retained within the pond result in high dinoflagellate proliferation. In contrast, in semi-enclosed ponds such as those at Douglas and Elbow Cays, brown pelicans provide the organic enrichment needed for dinoflagellate blooms to develop. Here benthic dinoflagellate species *G. polygramma* can form populations $>10^6$ cells/L that may dominate the waters (Morton and Villareal, 1999). Nutrients generated after a "bloom" would be retained because of the very low daily tides (20–25 cm) and calm wind conditions (Ellison et al., 1996; Villareal et al., this volume). Toxic *G. polygramma* red tides are known to cause extensive fish and shellfish kills (Taylor, 1962).

At Manatee Cay, mixotrophy was observed in an autotrophic species, *Gymnodinium sanguineum*, which engulfed smaller prey organisms (ciliates, pigmented nannoplankton, and microalgae). Here, *G. sanguineum* cells compete with heterotrophic grazers for the same food source (Bochstahler and Coats, 1993), as do harmful benthic species (*Gambierdiscus*, *Ostreopsis* and *Prorocentrum*) at South Water Cay (Faust, 1998). Mixotrophy is a recently described phenomenon (Jacobson and Anderson, 1986) that provides energy for cell growth, a potential advantage for dinoflagellates in nutrient-limited marine waters. As observed in this study, dinoflagellates can form "blooms" in oceanic oligotrophic mangroves. Therefore, by altering feeding behavior according to the available food sources, dinoflagellate populations can proliferate in many environments (Fenchel, 1988).

The autotrophic and heterotrophic dinoflagellate population of Pelican Cays is much

more diverse than previously suspected. Some species are conspicuous components of plankton assemblages and some tropically categorized as benthic (Table 1). Other species are rare and present in relatively low abundance. They are important components of the plankton and may play a pivotal role in food web interactions (Fenchel, 1988). Autotrophic and heterotrophic dinoflagellates are both affected by grazers. Ciliates, nannoplankton, and flagellates have been cited as important dinoflagellate consumers (Faust and Gullede, 1996; Jacobson and Anderson, 1986). Photosynthetic dinoflagellates consume small toxic dinoflagellates and prey on ciliates (Faust, 1998; Bockstahler and Coats, 1993; Hansen, 1991). The recent discovery of *Gymnodinium sanguineum* as a possible mixotroph at Manatee Cay may indicate that this species plays a dual role in the food web during high cell concentrations. The previously expected trophic role of ciliates and dinoflagellates thus appears reversed in the microscopic mangrove food web, as shown in estuarine assemblages (Bockstahler and Coats, 1993) and toxic species (Faust, 1998).

At present, it is difficult to explain the observed differences between species composition and collection sites. On some occasions, blooms are so profuse that they discolor the water. These are the most noticeable instances of the association between dinoflagellates and community dynamics, but there are many less spectacular occurrences that are part of the normal seasonal succession of dinoflagellates. The latter situation may not have as obvious an impact as a toxic bloom or a red tide, but its influence on food web dynamics may still be far reaching. In view of the central role played by dinoflagellates in the coral reef-mangrove microbial food web, they are able to explicitly exploit the environment to their benefit in order to survive and proliferate. The results of this study demonstrate that the Belizean coral reef-mangrove ecosystem is a delicate and species-rich environment and, as such, should be protected and preserved.

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APPENDIX

A list of armored dinoflagellate species recorded from the Pelican and associated Cays between 1994-1996 (* =photosynthetic species).

Taxa	Cat Cay	Douglas Cay	Elbow Cay	Fisherman's Cay	Lagoon Cay	Manatee Cay	Twin Cays
<i>Amphidinium carterae</i> *		+				+	+
<i>Blepharocystas</i> sp.*						+	
<i>Bysmatrum caponii</i> *		+	+			+	
<i>B. subsalsum</i> *	+		+	+		+	+
<i>Ceratium contortum</i> *				+		+	
<i>C. furca</i> *						+	
<i>C. hircus</i> *	+	+		+		+	+
<i>C. massilense</i> *						+	
<i>C. pentagonium</i> *						+	
<i>C. pulchellum</i> *		+				+	
<i>C. symmetricum</i> *						+	
<i>C. trichoceros</i> *	+	+		+		+	
<i>C. tripos</i> *	+					+	
<i>C. tripos</i> var. <i>atlanticum</i> *	+	+				+	
<i>Cochlodinium polykrikoides</i> *						+	+
<i>Coolia monotis</i> *						+	+
<i>Corythodinium</i> sp.*						+	
<i>Dinophysis acutoides</i>	+	+					
<i>D. caudata</i> *	+	+		+		+	+
<i>D. elongatum</i>						+	
<i>D. mitra</i> *	+				+		+
<i>D. rotundata</i>						+	+
<i>Dinophysis</i> sp.	+						
<i>Diplosalis assimetrica</i>		+			+	+	
<i>D. bomba</i>		+				+	
<i>D. lenticula</i>	+					+	
<i>Diplopelta symmetrica</i>	+	+					
<i>Diplopelta</i> sp.						+	
<i>Diplopsalopsis</i> sp.		+				+	
<i>Gambierdiscus australes</i> *	+	+				+	
<i>G. belizeanus</i> *						+	
<i>G. pacificus</i> *						+	
<i>G. toxicus</i> *	+		+	+	+	+	+
<i>Goitus</i> sp.			+				
<i>Goniodoma</i> sp.*		+					
<i>Gonyaulax diacanta</i> *				+		+	
<i>G. digitalis</i> *	+	+				+	

Appendix--continued

Taxa	Cat Cay	Douglas Cay	Elbow Cay	Fisherman's Cay	Lagoon Cay	Manatee Cay	Twin Cays
<i>G. fragilis</i> *	+	+				+	
<i>G. grindleyi</i> *		+	+			+	+
<i>G. monocanta</i> *	+		+			+	
<i>G. polygramma</i> *	+	+					
<i>G. reticulata</i> *			+				
<i>G. scrippsiae</i> *			+				
<i>G. spinifera</i> *	+	+			+	+	+
<i>G. vrior</i> *		+	+				
<i>Gonyaulax</i> sp.*			+				
<i>Gymnodinium sanguineum</i> *		+				+	+
<i>Gymnodinium</i> sp. 1*						+	
<i>Gymnodinium</i> sp. 2*						+	
<i>Heteraulacus sphericus</i>		+				+	
<i>Lingulidinium polyedra</i> *	+	+		+		+	
<i>Noctiluca</i> sp.*				+			
<i>Ostreopsis labens</i> *		+	+			+	
<i>O. lenticularis</i> *		+	+			+	
<i>O. mascarenensis</i> *		+	+			+	
<i>O. ovata</i> *		+	+			+	
<i>O. siamensis</i> *		+	+			+	
<i>Peridiniella spaeroidea</i> *						+	
<i>Peridinium venestrum</i> *	+	+				+	
<i>P. divergens</i> *						+	
<i>P. ovatum</i> *						+	
<i>Phaeopolykrikos</i> sp.*						+	
<i>Plagonidium belizeanum</i> *						+	
<i>Podolampas elegans</i>		+					
<i>Podolampas</i> sp.		+					
<i>Prorocentrum belizeanum</i> *				+			+
<i>P. caribbeanum</i> *						+	+
<i>P. concavum</i> *							+
<i>P. elegans</i> *			+				+
<i>P. emarginatum</i> *			+				+
<i>P. formosum</i> *			+				+
<i>P. foraminosum</i> *			+				+
<i>P. gracile</i> *						+	
<i>P. hoffmannianum</i> *				+		+	+
<i>P. lima</i> *		+	+			+	+
<i>P. maculosum</i> *			+	+		+	+
<i>P. mexicanum</i> *		+	+			+	+
<i>P. micans</i> *						+	

Appendix--continued

Taxa	Cat Cay	Douglas Cay	Elbow Cay	Fisherman's Cay	Lagoon Cay	Manatee Cay	Twin Cays
<i>P. norriseanum</i> *		+				+	
<i>P. ruetzlerianum</i> *							+
<i>P. triestum</i> *						+	
<i>Prorocentrum</i> sp.*						+	
<i>Protoceratium excentricum</i> *	+					+	
<i>P. reticulatum</i>						+	
<i>Protopteridinium crassipes</i>	+					+	
<i>P. elegans</i>	+					+	
<i>P. depressum</i>	+	+		+		+	
<i>P. diabolium</i>	+			+		+	
<i>P. divergens</i>	+	+		+		+	
<i>P. oblongum</i>	+	+				+	
<i>P. oceanicum</i>	+	+				+	
<i>P. pallidum</i>	+	+				+	
<i>P. pellucidum</i>						+	
<i>P. punctulatum</i>						+	
<i>P. pyrum</i>				+		+	
<i>P. quinquecorne</i>		+					+
<i>P. reticulatum</i>	+	+					+
<i>P. steidingeriae</i>		+		+		+	
<i>P. tumidum</i>	+			+			
<i>P. steinii</i>						+	
<i>Pyrodinium bahamense</i> var. <i>bahamense</i>	+	+	+	+		+	
<i>P. var. compressum</i> *		+				+	
<i>Pyrophacus horologium</i> *		+				+	
<i>Protoceratium</i> sp. cf. <i>steinii</i> *		+	+		+	+	+
<i>P. steinii</i> var. <i>vacampoae</i> *						+	
<i>Scrippsiella trifida</i> *						+	
<i>S. trochoidea</i> *							+
<i>Sinophysis microcephalus</i>							+
<i>Zygabikoniidum</i> sp.		+				+	